

Sirex wasp fungus -*Amylostereum areolatum*

Amylostereum areolatum is a basidiomycete that causes a serious white rot of a broad range of conifers. This fungus forms a symbiotic association with woodwasps of the genus *Sirex*. The species *Sirex noctilio* Fabricius is listed as 'highly invasive' on the ISSG/IUCN website (ISSG, 2008) and is a Regulated Pest for the United States (APHIS, 2009). The wasp and the fungus are native to Europe, North Africa and western Asia where their damage is considered secondary. (Spradbery and Kirk, 1978). When introduced to areas of the Southern Hemisphere where exotic pine species are grown in plantations, these organisms have caused major losses. The insect invaded New Zealand by 1900, but did not cause serious concern until the 1940s (Talbot, 1977). It later spread to Tasmania and the southern parts of Australia and the wasp/fungus association was introduced into southern South America. Invasion of South Africa occurred in 1994 (Tribe, 1995). Woodwasps are repeatedly detected in material imported to the USA, but were successfully excluded until 2004 (Wilson et al, 2009). The wasp and fungus were found in Canada (Ontario) and New York (Bergeron et al., 2008; Wilson et al, 2009). Recent surveys found the wasp in four states of the USA (Evans-Goldner and Bunce, 2009) and 25 counties of Ontario in Canada (Shields, 2009).

Amylostereum areolatum (Chaillet ex Fr. : Fr.) Boidin ex J. Erikss., Hjortstam & Ryvarden 1978

Symptoms on infected trees are a combination of those caused by the fungus and wasp vector. Resin droplets appear at sites of wasp oviposition (Kobayashi et al., 1978; King, 1966). On *Pinus radiata* yellowing of needles occurs on older parts of the tree within several weeks, followed by yellowing and loss of needles on younger parts, or death of the tree with foliage remaining green or turning red-brown. The yellowing of younger needles is sometimes accompanied by wilting of the youngest ones at branch tips, the whole fascicle drooping, particularly in periods of active growth and adequate moisture (Coutts, 1969). These symptoms, however, are due to a mucus material produced by the wasp, not the fungus (Coutts, 1969; Talbot, 1977).

Interior symptoms begin with a white discoloration of the wood, extending more longitudinally than laterally, produced beyond the growth of the fungus near the oviposition site. A brown-stained area of similar shape develops later in the bark around the site; a strip of dead bark develops above and below the wasp puncture. *Amylostereum areolatum* causes a dry white rot of the wood before and after the death of the tree (King, 1966).

Fruiting bodies perennial on conifers, corky or leathery, partly resupinate, flattened on bark or wood with hymenium exposed, partly reflexed, with shield-shaped or broad areas projected 1-3 cm upwards/outwards. Upper/outer surface rust brown to black, matted-hairy, undulating, with furrows or grooves. Hymenial surface generally smooth, sometimes cracked or uneven, gray to brown with a violet or lilac tint, margin thin, white. Basidia in hymenium narrowly clavate, 20-30 x 4-5µm; basidiospores smooth, colorless, ellipsoidal to cylindrical, amyloid (staining blue in iodine). Context dimitic; cystidia encrusted, 40-60 x 6-9 µm. Thomsen (1998) found the hymenium of a limited sample of basidiocarps to be brown-violet, with a white margin; basidiospores were 3.6-5.6 x 2-3.2 µm.

Colony in culture relatively fast-growing, white, cottony, becoming more appressed and dark, cream, buff or brownish, with age, darker on reverse. Mycelium dimitic: generative hyphae thin-walled, with clamp connections, skeletal hyphae thick-walled, generally unbranched, ending in thick-walled, brownish, encrusted cystidia. Arthrospores cylindrical, hyaline, generated from certain hyphae by fragmentation. Optimum growth in culture occurred at 20-25 C (King, 1966).

Fungus in hypopleural organs of siricid larvae consists of coiled hyphae surrounded by a waxlike material. In the intersegmental sacs, or mycangia, of adult females, arthrospores are unicellular or multicellular (Gilmour, 1965).

See Boidin and Lanquetin (1984; Breitenbach and Kranzlin (1984), Chamuris (1988), and Gadgil (2005) for more detailed descriptions. Stalpers (1978) provides a description of the asexual state.

Host range: Known primarily on members of the Pinaceae, although also reported on Cupressaceae (Cryptomeria) and Taxodiaceae.

Geographic distribution: Vectored by the wasp *Sirex noctilio*; also *S. juvencus* L. and *S. nitobei*. Native to Europe, North Africa and western Asia, although more commonly seen in central Europe than in the northern countries. The wasp has recently invaded parts of the northern United States and adjacent Canada (Bergeron et al., 2008; Wilson et al., 2009). Reported in Japan (Fukuda and Hijii, 1996), northwestern China (Zhang, 2005) and the Russian Far East (Boidin and Lanquetin, 1984).

Illustrations available at http://www.gobe.si/slike/thumb_Amylostereum_areolatum.jpg See also http://www.gobe.si/slike/thumb_Amylostereum_areolatum.jpg

Notes: The genus *Amylostereum*, including *A. areolatum*, was separated by Boidin (1958) from *Stereum* on the basis of the encrusted cystidia in the hymenium. *Lloydellopsis* is a redundant later genus, based on the same type species. *Xylobolus* is another group of *Stereum*-like fungi having smooth amyloid basidiospores that is distinguished from *Stereum* and *Amylostereum* principally by the presence of acanthophyses in the hymenium (Boidin, 1958).

Amylostereum currently contains four species (Kirk et al., 2008). *A. areolatum*, *A. chailletii* (Pers.) Boidin and *A. laevigatum* (Fr. ex Fr.) Boidin have symbiotic relationships with woodwasps in the family Siricidae (Gilbertson, 1984; Tabata and Abe, 1997).

Tabata et al. (2000) examined relationships of *Amylostereum* and *Echinodontium* species using sequences of ITS and manganese peroxidase regions of DNA. Their results confirm relationships within *Amylostereum* (Vasiliauskas et al., 1999; Slippers et al. 2000), grouping the other three species together at some distance from *A. Amylostereum*. With respect to the genus as a whole, they proposed placing it in the family Echinodontiaceae rather than in its own family, although that is not accepted here.

Similar species: *Amylostereum areolatum* is similar to *A. chailletii* (Pers.:Fr.) Boidin, also a woodwasp-vectored fungus in Northern Hemisphere forests. These species are distinguished by larger basidiospores, 6.2-8 x 3-4 µm, according to Boidin and Lanquetin (1984), although Thomsen (1998) found a range of 4.8-8 x 2.4-4 µm and Chamuris (1988) reports 5-8 x 3-5 µm. Thomsen (1998) describes the hymenium color of fruiting bodies as varying in pale to darker brown shades (cream, orange grey, reddish-brown, grayish-brown or brick red) without the purple or lilac tint of *A. areolatum*; the paler colors are most common. Cultures on 5 % MEA or 4% PDA are paler than those of *A. areolatum* (pale yellow or yellowish white vs. yellow-brown to rust brown) and do not produce arthrospores (although spores are found in wasp mycangia in *A. chailletii*) (Thomsen, 1998). King (1966) reported that many basidiospores of *A. chailletii* germinated and produced mycelium on agar, while those of *A. areolatum* seldom germinated and, if so, did not produce mycelium.

Distribution: The fungus and wasp larvae were introduced into New Zealand before 1900, apparently in shipments of logs from Europe (Gilmour, 1965). This was not of great concern until damage to exotic tree plantations appeared in the drought years of the late 1940s (Rawlings, 1955). In 1950-51, the wasp/fungus appeared in Tasmania (Gilbert and Miller, 1952). By 1961 they had arrived in Victoria eventually reaching New South Wales and Southern Australia (Carnegie et al., 2005). Despite the awareness of its threat, the wasp/fungus was introduced into South America, beginning in Uruguay in 1980, spreading to Argentina, Brazil, and Chile (Ciesla, 2003). Invasion of South Africa occurred in 1994 (Tribe, 1995). Woodwasps are repeatedly detected in material imported to the US, but *S. noctilio* was successfully excluded until 2004 (Ciesla, 2003; Wilson et al., 2009). The wasp and fungus were later found in nearby Canada (Ontario) though apparently due to a separate introduction (Bergeron et al., 2008; Wilson et al., 2009). Recent surveys found the wasp in four states of the USA (Evans-Goldner and Bunce, 2009) and 25 counties of Ontario in Canada (Shields, 2009).

The most recent introductions into the United States and Canada indicate the level of risk for this pest/pathogen threat. Despite a high level of awareness and frequent interceptions of woodwasps by plant protection personnel (Ciesla, 2003), the wasp and fungus have arrived in North America. The likely routes and means were not identified (Bergeron et al, 2008; Wilson et al, 2009). Ciesla (2003) cites a number of consumer goods that incorporate logs or wood products as potential carriers. Bark-bearing and debarked logs, as well as untreated lumber, might carry the fungus, but the wasp appears necessary for its inoculation into trees. Once introduced, the wasp, a strong flier seeking out suitable tree hosts (Ciesla, 2003), can transport the fungus over land and possibly across narrow seas. Northwestern South America, eastern Africa, and western Australia are areas for which accidental introduction by humans would be required (Carnegie et al., 2006).

In Europe, the fungus may eventually produce fruiting bodies on infected trees. Elsewhere, observation of holes made by emerging siricid wasps are a clue to presence of the fungus associated with larval tunnels (Spradbery and Kirk, 1978; Schiff, 2008). Since there may be more than one species of woodwasp in a given area, examination of culture characteristics or DNA sequence data is required to establish the identity of the fungus.

Diagnostic methods: The production of arthrospores in culture is necessary to identify *A. areolatum* (Gaut, 1969). These appear in cultures grown on standard fungal media, including 2% malt extract agar and cornmeal agar (Stalpers, 1978; King, 1966). Gaut (1969) utilized matings of homokaryotic cultures, observation of hyphal anastomosis, and electrophoretic protein profiles to identify the pathogen in Australia. Bergeron et al. (2008) compared the ITS sequences of rDNA extracted from cultured isolates with those of standard strains of *A. areolatum*. The Canadian isolates matched European and Asian isolates at the 99% level; they matched *A. chailletii* at about 97%. Sequences of the ITS region for *A.*

areolatum and *A. chailletii* are deposited in GenBank (Tabata et al., 2000). Slippers et al. (2002) found that RFLP analysis of DNA easily distinguished the two species.

Host susceptibility: In Europe, the fungus is reported on *Abies*, *Picea*, (Hansen & Knudsen, 1997) and *Cryptomeria* species (Cardosa et al., 1992). Gadgil (2005) considers the introduced species of *Abies*, *Larix* and *Picea* relatively resistant in New Zealand, but the introduced species of *Pinus* are generally susceptible. *Abies holophylla* is a susceptible native species in the Russian Far East (Boidin and Lanquetin, 1984). In Japan, *Pinus densiflora* and *P. thunbergii* are hosts (Kobayashi, 2007); the fungus is reported from China on a *Picea* sp. (Zhang, 2005). *Pseudotsuga menziesii* (Gilmour, 1965) and *Cedrus atlantica* are also hosts in New Zealand (Burnip et al., 2008). The tree species known to be attacked by *Sirex noctilio*, thus also hosts for this fungus, are listed by CABI (2009).

King (1966) reported that the fungus also grew well, though more slowly, in laboratory-inoculated freshly cut branches of pine species: *P. radiata* L., *P. canariensis* C. Sm., *P. pinaster* Ait., and *P. halepensis* Mill., and of other conifers: *Araucaria cunninghamii* Sweet., *A. excelsa* R. Br., and *Cedrus deodara* (Roxb.) Loud.,

Biology and Ecology: *Amylostereum areolatum* has a tetrapolar outcrossing mating system (Vasiliauskas and Stenlid, 1999). The species also exhibits vegetative compatibility groups in culture (Vasiliauskas and Stenlid, 1999), which appear to represent genetic clones (Vasiliauskas et al., 1998).

The fungus is not known to fruit in Australia or New Zealand (King, 1966; Hood, 1992), although isolates from infected trees were able to fruit on wood blocks in culture (Gaut, 1969). Arthrospores carried by adult female wasps are injected into trees during oviposition. Neither arthrospores nor basidiospores were able to grow beyond germination in pure culture, but Gaut (1969) was able to obtain cultures from arthrospores by starting them on a tissue culture of *Pinus radiata*. The sexual state is observed in nature in central Europe (Breitenbach and Kranzin, 1988), though it is rare in northern Europe (Eriksson et al., 1978). Based on the low number and wide distribution of vegetative compatibility groups around the Baltic Sea, Vasiliauskas and Stenlid (1999) and Thomsen and Koch (1999) considered distribution of the pathogen in that region more likely to have occurred through the *insect* vector than by aerial dispersal of basidiospores.

Based on cultural tests, King (1966) suggested that *A. areolatum* is a poor competitor for growth in *Sirex*-infested trees; poor competition with saprobes in dead trees may explain the low frequency of fruiting. *A. areolatum* grows slowly in the tree and only in dry wood (70% moisture content (Gaut, 1969; Webber and Gibbs, 1989). The fungus colonies are limited to areas around the oviposition site and larval tunnels while the tree is alive (King, 1966) and do not grow much beyond the inoculation site in resistant trees (Coutts, 1969). Nevertheless, Klepzig et al. (2009) found that in culture *A. areolatum* can exclude the *Ophiostoma* species associated with the southern pine beetle, indicating that it might be successful in early competition in infected trees.

Strains of the fungus may differ. Williams and Mastro (2009) report a significant growth rate difference between a North American isolate and one used in Australian biological control work. The Australian isolate is different from the single clone which was introduced with the wasp into South Africa and South America (Slippers et al., 2001).

Associations: The fungus has a mutualistic association with *Sirex* spp.: *S. noctilio* Fabricius, *S. juvencus*, *S. notobei* Matsumura (Gilbertson, 1984). It is carried in specific structures (mycangia) on the female woodwasp body at the base of the ovipositor, and is introduced into the holes drilled by the wasp when it is laying eggs, although, in some cases, only the spores will be deposited (Gaut, 1969; Fukuda and Hijii, 1996).

The fungus grows in a limited area around the hole, rotting the sapwood, and providing a dry, resin-free habitat for the wasp larvae, which tunnel in the wood and feed on the mycelium (Madden, 1981; Webber and Gibbs, 1989). When fungal growth results from wasp deposits of spores alone in relatively healthy trees, this may weaken the trees sufficiently to provide additional breeding sites for the wasp (Gilbertson, 1989; Fukuda and Hijii, 1996).

Wasp larvae carry hyphae encased in a wax-like material inside hypopleural organs on the exoskeleton, but these are absent in the pupae (Gilmour, 1965). The adult female then must acquire quantities of hyphae as it is emerging from pupation and out of the tree (Webber and Gibbs, 1989). Male larvae and adults do not carry the fungus.

Tabata et al (2000) have reported the isolation of *A. areolatum* from another siricid species, *Xoanon matsumurae* in Japan, but the details of the association were not explored.

Movement and dispersal: Basidiospores are distributed by wind from the fruiting bodies produced on the outside surface of erect or fallen trees (Breitenbach and Kranzlin, 1988). Basidiocarps are rare in northern Europe (Eriksson et al., 1978). Vasiliauskas and Stenlid (1999) and Thomsen and Koch (1999)

suggest this means of dispersal is unlikely to account for trans-Baltic occurrence of clones of this species. Instead, the fungus is likely to be wasp-transmitted across significant distances, but probably carried across international boundaries in imported wood. Basidiocarps have not been observed in overseas areas of introduction (King, 1966; Hood, 1992), thus basidiospores are not a significant means of spread there.

The siricid wasps are strong fliers, capable of flying several kilometers in search of suitable trees (Ciesla, 2003). A natural spread rate of 20-50 km per year has been reported for *Sirex noctilio* (CABI, 2009). The wasp generally attacks weakened, damaged or poorly growing trees (Talbot, 1977). Fukuda and Hijii (1998) report that the species *S. nitobei* also oviposits on weakened trees, apparently detecting these by of volatile compounds. Weakened trees produce a greater quantity of volatiles (Borockzy et al., 2009).

The fungus is considered to have been introduced into New Zealand with *Sirex noctilio* in a shipment of logs (Gilmour, 1965), and with the wasp into South Africa in wooden packing crate material (Tribe and Cillie, 2004). Siricid wasps in wood products have been intercepted by APHIS in the USA (Ciesla, 2003) and by phytosanitary agencies in other countries (CABI, 2009).

Impact: Economic effects of the introduction of the *Sirex noctilio*/*Amylostereum areolatum* complex in countries of the Southern Hemisphere are summarized by CABI (2009). Haugen (2006) reports some projections of possible impacts on forests of the United States, and Yemshanov et al., (2009) have presented models of possible impacts on the forest industry in eastern Canada. The total harvest losses over 28 years in Canada could equal as much as \$2.1 billion depending on model assumptions.

Talbot (1977) notes that the impact of the *Sirex*/*Amylostereum* association can vary depending on the silvicultural situation. The fungus is relatively rare in Europe, where the several *Amylostereum* species/siricid wasp associations are presumably in balance in the natural woodland. In plantations of exotic species, however, this balance may be disrupted. Vasiliauskas et al. (1996) report *A. areolatum* as one of the primary parasites on wounded trees in Swedish plantations. The large outbreak of *Sirex noctilio* in 1946-49 in New Zealand, despite the significant number of trees killed, may have had a beneficial effect by reducing the density of the long-unthinned plantations of *Pinus radiata* (Rawlings, 1955). Eliminating the more susceptible smaller and weaker trees through thinning is a tactic to reduce the severity and impact of the fungus/wasp association on plantations in Australia (Neumann and Marks, 1990). In the USA and Canada, a number of native species, some of which are attacked as exotics in overseas plantations, may be threatened (Wilson et al, 2009), particularly where they occur in denser stands or are grown in plantations in southern states (Dodds, 2009). The existing complex ecological situation that is more similar to that of the fungus's native range, may reduce or complicate the impact (Schiff, 2008).

Effects in the southern hemisphere have focused primarily on introduced tree species. No data are available on the impacts on the native species in forests in Japan (Kobayashi et al., 1978; Fukuda and Hijii, 1996). Haugen (2006) identified possible impacts in the United States through changes in forest composition, reduction in native siricid wasp populations, and increases in other insect pests and fungal pathogens that attack weakened or dying trees.

Prevention: Despite the history of accidental introduction of the fungus/wasp association to widely separated continents, phytosanitary measures may prevent, or at least slow, their spread by intercepting infested logs, packing materials, and other bark-bearing tree products (Ciesla, 2003; Evans-Goldner and Bunce, 2009). Human-assisted transport of these organisms is required for movement to other parts of those continents where climatic conditions and tree species permit their establishment (Carnegie et al., 2006). Efforts to prevent that transport are conducted by phytosanitary agencies such as APHIS Plant Protection and Quarantine (2009) and the Canadian Food Inspection Agency (2009).

Control: Silvicultural practices, including selection of suitable tree species and phenotypes, choice of proper plantation sites, appropriate and timely thinning of stands, prevention of wounds caused by fire or harvesting, removal of cut, damaged and windthrown trees and sufficient fertilization, will reduce or prevent the accumulation of weakened or dying trees that are the preferred breeding sites for siricid wasps (Neumann and Marks, 1990; CABI, 2009).

CABI (2009) lists parasitic and predatory insects that attack *Sirex noctilio*, most of which have been deployed in Australia and New Zealand. One parasitoid moves toward fungus-produced volatiles to locate the larvae on which its own young feed (Martinez et al., 2006). Parasitoids provide limited control of wasp populations because they depend on a certain level of siricid population for their own survival and multiplication (Carnegie et al., 2005).

The tylenchid nematode *Beddingia* (= *Deladenus*) *siricidicola*, discovered in New Zealand and later found in Europe (Bedding, 1995), lives in and feeds on *A. areolatum* colonies in trees and also infects *Sirex* larvae and female wasps. Because it has a separate cycle of growth and reproduction based on fungus feeding, it can cause a greater reduction in wasp numbers. The nematode can be raised in cultures of the

fungus and injected into trees for effective control of the wasp (Bedding, 1995). *Beddingia siricidicola* is currently under evaluation for use in the United States (Williams and Mastro, 2009); it is already present in infected trees in Canada (Shields, 2009).

Monitoring: CABI (2009) outlines the use of trap trees, in combination with remote sensing surveys, for identifying the areas of infestation by *Sirex noctilio* and monitoring its activity. Carnegie et al (2005) discuss their use in Australia.

References

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